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Climatic variability and hemispheric differences in insect cold tolerance: support from southern Africa

B. J. SINCLAIR*† and S. L. CHOWN

Spatial, Physiological and Conservation Ecology Group, Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland, 7602, South Africa

Summary

1. Insects generally survive subzero temperatures by utilizing either freeze tolerance or freeze avoidance. Comparative analyses from a limited data set have indicated that freeze tolerance may be predominant among species at temperate latitudes in the southern hemisphere, while freeze avoidance dominates in the north.
2. We investigated the cold tolerance strategies of cockroaches and beetles from cold regions in southern Africa, including the Cederberg mountains, the Karoo desert and the Drakensberg mountains.
3. We found that 8 of 11 species are freeze tolerant.
4. Overall, 77% of species investigated in the southern hemisphere ($n = 27$) were freeze tolerant, which is significantly different from the 29% ($n = 258$) in the north ($P < 0{\cdot}001$).
5. There are regular, unpredictable subzero temperature events in the southern African habitats; such variability appears to be a general feature of many cold habitats in the southern hemisphere, which may lead to the observed interhemispheric discrepancies in cold-tolerance strategies.

Key-words: Freeze avoidance, freeze tolerance, macrophysiology, microclimate, rapid cold-hardening

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Introduction

There is much speculation and increasing evidence that species in the northern and southern hemispheres respond differently to changes in latitude and season, with smaller magnitude, less predictable, responses in the south compared with the north (Chown *et al*. 2004). The evidence includes frost tolerance of alpine trees (Feild & Brodribb 2001), avian reproductive strategies (Russell 2000; Russell, Yom-Tov & Geffen 2004) and geographic variation in plant and animal range sizes (Blackburn & Gaston 1996; Gaston & Chown 1999). Hemispheric differences in biological features are thought to be a consequence of very different general climates associated with the preponderance of ocean in the south (Gaston & Chown 1999). Compared with the mostly continental northern hemisphere, the temperate latitudes in the south have truncated temperature extremes, mild winter temperatures and reduced seasonality (Bonan 2003).

Mild temperatures in south temperate habitats result in winter mean temperatures that are often close to 0 °C (Bonan 2003), and this means that both inter- and intra-annual variations in temperature affect the frequency with which the freezing threshold is crossed. Cold climates in temperate regions of the southern hemisphere are thus characterized by repeated freeze–thaw cycles, which may occur year-round, resulting in both freezing events in the summer and above-zero temperatures in the winter (Bliss & Mark 1974; Mark 1994; Ramløv 1999; Mark, Dickinson & Hofstede 2000; Feild & Brodribb 2001; Boelhouwers & Meiklejohn 2002; Boelhouwers, Holness & Sumner 2003; Bonan 2003). In insects, those southern species that inhabit these environments and are capable of surviving subzero temperatures should adopt a strategy that enables them both to survive unpredictable summer cold snaps, without the subsequent costs of injury or death from gut-initiated freezing in feeding individuals when temperatures retreat below zero, and to take immediate advantage of warm spells in winter temperatures for feeding and growth. There are several strategies that enable insects to survive subzero temperatures (Bale 2002; Holmstrup, Bayley & Ramløv 2002), but only two of these meet the above criteria: freeze tolerance, where individuals can survive internal ice-formation, thus nullifying mortality associated with freezing, and rapid cold-hardening associated with freeze avoidance (Lee, Chen & Denlinger 1987; Bale 2002; Sinclair *et al*. 2003b). Quantitative analysis of published cold-hardiness

†Author to whom correspondence should be addressed. E-mail: celatoblatta@yahoo.co.uk
*Present address: Department of Biological Sciences, University of Nevada, Las Vegas, NV 89154–4004, USA.

strategies (Sinclair, Addo-Bediako & Chown 2003a) has indicated that freeze tolerance predominates in southern hemisphere insects (85% of species *vs* 29% in the northern hemisphere, $P < 0{\cdot}0001$). However, this inference is weakened by small sample size in the southern hemisphere ($n = 13$ species from the south, 241 from the north), and a data set largely restricted to cold islands (Sinclair *et al*. 2003a). If this pattern is more general, then for all regions of the southern hemisphere cold-hardy insects should typically show freeze tolerance, or evidence of rapid cold-hardening in the absence of freeze tolerance. Here we test the former prediction for southern Africa, a region not represented in previous analyses (see Addo-Bediako, Chown & Gaston 2000; Sinclair *et al*. 2003a).

Materials and methods

To determine cold-tolerance strategies of insects from a predominantly hot continent, we collected insects from three habitats in southern Africa where they were likely to be regularly exposed to subzero temperatures. These were in the high elevation Karoo desert at Ezeljacht farm near Sutherland, Northern Cape Province, South Africa (1550 m a.s.l., 32·4105° S 20·57747° E; permit no. 058/2003); near the summit of Sneeukop in the Cederberg mountains, Western Cape Province, South Africa (1800–1926 m a.s.l., 32·35512° S 19·16155° E; permit no. 234/2001); and at high elevations in the Sani Pass area of the Drakensberg mountains, KwaZulu-Natal, South Africa (2900–3200 m a.s.l., 29·58448° S 29·2889° E; permit no. 2982/2003).

MEASUREMENT OF MICROCLIMATE TEMPERATURES

Microclimate temperatures were measured beneath rocks representative of those lifted to search for insects in the vicinity of the area where collections were made at each site. Temperatures were recorded hourly by iButton thermochron dataloggers (±0·5 °C; Dallas semiconductors, Dallas, TX) (Karoo and Drakensburg sites), or half-hourly, using a TMCx-HA thermistor probe attached to a Hobo H8 series datalogger (±0·1 °C; Onset Computer corporation, Pocasset, MA) (Cederberg site). Air temperatures were monitored half-hourly at each site using shielded TMCx-HA thermistor probes attached to a Hobo H-8 logger. Sani Pass (2982 m), the site for air temperature measurements in the Drakensberg is some 200 m lower than the rock logger site. Mean, maximum and minimum air temperatures are presented from a 1-year period over 2003–04 from each site (with the exception of the Drakensberg, for which data from June and July are unavailable). Long-term winter air temperature recordings are not yet available for these sites, but representative means for winter periods are given for each of them (June, July and August 2003 for the Karoo site; June and July 2003 for the Cederberg site and August 2003 for the Drakensberg site).

INSECT COLLECTION AND MAINTENANCE

Insects were collected from beneath rocks on rock outcrops or by live pitfall trapping (with apple baits) as outlined in Table 1. Abundant species were chosen so that 50–300 individuals could be captured within a few days of collecting. Animals were returned to the laboratory in insulated boxes, and maintained in the dark in a refrigerator (6 ± 1 °C) with twigs and soil from the collection site and fresh apple as a source of food and moisture until they were used in experiments (not more than 2 weeks for beetles, up to 2 months for cockroaches, which grow, moult and reproduce readily in the laboratory. Cockroaches were also provided with fragments of dry horse feed pellets). Cockroaches and beetles were weighed to ±0·1 mg (Mettler-Toledo AX504, Mettler, Columbus, OH) and dry masses of most species determined after drying for 3 days at 60 °C. Voucher specimens of the cockroach species are lodged in Iziko Museums of Cape Town (accession numbers in Table 1), while the beetles are lodged in the South African National Arthropod collection (accession numbers in Table 1).

DETERMINATION OF COLD-TOLERANCE STRATEGY

Insects were placed in 1·5-ml tubes in contact with a 40 swg type T (copper–constantan) thermocouple, and cooled to a series of subzero temperatures in a Peltier-controlled cooling device at 0·1 °C min^{-1} (closer to ecologically relevant cooling rates than the more usual 1 °C min^{-1}, see Chown & Nicolson 2004), and held for 1 h at the test temperature. Test temperatures were decided dynamically on the basis of survival of a species, with the aim of spanning temperatures that resulted in 100% survival and 100% mortality to allow estimation of the temperature at which 50% mortality may be expected (LT_{50}). Freezing of insects was detected from the heat release associated with the latent heat of crystallization, and could be assigned to individual animals, allowing the determination of temperatures of crystallization (T_c) (normally distributed, shown as mean ± standard error), LT_{50} (calculated using logistic regression on Statistica v 6·1, standard errors calculated from error estimates on slope and intercept from the model) and lower lethal temperature (LLT) (0·1 °C lower than the lowest temperature survived by an individual of a species). It was also possible to directly associate freezing of insects with their survival, and species were scored as freeze tolerant or freeze intolerant on the basis of the recovery of individuals in which ice formation was recorded. Survival was scored after 48 h, and individuals that could not right themselves or move in a coordinated fashion because of their injuries were scored as dead. Survival of the tenebrionids was determined from overnight righting response, and response to stimulus (scratching the abdomen with a pair of fine forceps).

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Table 1. Cold tolerance and collection information for 11 species of southern African insects

Species (accession number)	Source	Fresh mass (g) ± SEM (*n*)	Dry mass (g) ± SEM	T_c ± SEM (°C) (*n*)	LT_{50} (°C) ± SEM	LLT	Cold-tolerance strategy
Coleoptera*:* Tenebrionidae							
Pimeliinae							
Afrinus sp. (AcP 9494)	K – stones	0·0156 ± 0·0011 (15)	0·0056 ± 0·0004	−6·8 ± 0·1 (25)	−6·8 (−6·9, −6·7)	−7·9	FA
Stenocara dentata (AcP 9495)	C – pitfalls	0·2239 ± 0·0196 (13)	0·0882 ± 0·0062	−6·6 ± 0·4 (26)	−6·8 (−9, −4·7)	−8·9	FA
cf. *Somaticus* sp. (AcP 9497)	K – pitfalls	0·1370 ± 0·0125 (10)	0·0373 ± 0·0031	−5·4 ± 0·2 (37)	−6·4 (−9·5, −3·2)	−7·8	FT
Tenebrioninae							
cf. *Planostibes* sp. (AcP 9493)	K – stones	0·0483 ± 0·0031 (11)	nd	−7·2 ± 0·4 (17)	−6·9 (−6·9, −6·7)	−7·6	FA
cf. *Psorodes* sp. (AcP 9496)	C – stones	0·1638 ± 0·0108 (10)	0·0544 ± 0·0044	−4·9 ± 0·2 (28)	−6·5 (−8·4, −4·7)	−7·1	FT
Coleoptera: Carabidae							
Pterostichini sp. (AcP 9498)	D – stones	0·0470 ± 0·0019 (60)	0·0176 ± 0·0006	−3·0 ± 0·1 (60)	−4·4*	−5·1	FT
Blattodea: Blaberidae Perisphaeriinae							
cf. *Perisphaeria* sp. 1 (SAM-BLA-A000493 to A000498)	D – stones	0·3492 ± 0·0369 (10)	0·0974 ± 0·0136	−4·3 ± 0·1 (88)	−9·7 (−9·8, −9·6)	−11·3	FT
cf. *Perisphaeria* sp. 2 (SAM-BLA-A000499 to A000501)	K – stones	0·6708 ± 0·0340 (15)	nd	−5·9 ± 0·2 (8)	<–8·6**	<–8·6	FT
cf. *Perisphaeria* sp. 3 (SAM-BLA-A000502 to A000506)	C – stones	0·4735 ± 0·0233 (35)	nd	−5·0 ± 0·1 (19)	−8·0**	−7·9	FT
cf. *Derocalymma* sp. 1 (SAM-BLA-A000507 to A000511)	C – stones	0·2287 ± 0·0270 (10)	0·0742 ± 0·0093	−4·3 ± 0·3 (57)	−6·15 (−6·2, −6·1)	−6·7	FT
cf. *Derocalymma* sp. 2 (SAM-BLA-A000512 to A000514)	K – stones	0·2248 ± 0·0221 (15)	nd	−5·3 ± 0·4 (10)	−7·1 (−7·1, −7·0)	−6·8	FT

Source: K – Karoo, C – Cederberg; D – Drakensberg; (further site information in methods). nd indicates that dry mass was not determined for a species. Cold-tolerance strategies: FT – freeze tolerant, FA – freeze avoiding. T_c = temperature of crystallization. Accession numbers are for Iziko Museums of Cape Town (Blattodea) or the South African National Arthropod Collection (Coleoptera).
*LT_{50} values for which the standard error encompassed < 0·1 °C.
**LT_{50} values for which standard error could not be estimated by logistic regression.

Table 2. New species added to the insect cold-tolerance strategies database

Species	Family	Order	Strategy	Latitude (°)	Reference
Heleomyza borealis	Heleomyzidae	Diptera	FT	−78	Worland, Block & Grubor-Lajsic (2000)
Phytomyza ilicis	Agromyzidae	Diptera	FA	−53	Klok, Chown & Gaston (2003)
Aphidius ervi	Braconidae	Hymenoptera	FA	−50	Langer & Hance (2000)
Aphidius rhopalosiphi	Braconidae	Hymenoptera	FA	−50	Langer & Hance (2000)
Diplolepis spinosa	Cynipidae	Hymenoptera	FA	−50	Williams, Shorthouse & Lee (2002)
Diplolepis gracilis	Cynipidae	Hymenoptera	FA	−50	Williams *et al.* (2002)
Trichius fasciatus	Cetoniidae	Coleoptera	FA	−48	Vernon & Vannier (2001)
Periclistus pirata	Cynipidae	Hymenoptera	FA	−46	Williams *et al*. (2002)
Diplolepis polita	Cynipidae	Hymenoptera	FA	−46	Williams *et al*. (2002)
Dendroctonus ponderosae	Scolytidae	Coleoptera	FA	−43	Bentz & Mullins (1999)
Aphidoletes aphidimyza	Cecidomyiidae	Diptera	FT	−42	Kostál & Havelka (2000)
Pyrrharctia isabella	Arctiidae	Lepidoptera	FT	−41	Layne, Edgar & Medwith (1999)
Phyllonorycter ringoniella	Gracillariidae	Lepidoptera	FA	−39	Li, Oguchi & Goto (2002)
Liriomyza huidobrensis	Agromyzidae	Diptera	FA	−39	Chen & Kang (2002)
Tribolium castaneum	Tenebrionidae	Coleoptera	FA	−38	Burks & Hagstrum (1999)
Oryzaephilus surinamensis	Cucujidae	Coleoptera	FA	−38	Burks & Hagstrum (1999)
Cryptolestes ferrugineus	Cucujidae	Coleoptera	FA	−38	Burks & Hagstrum (1999)
Sitophilus oryzae	Curculionidae	Coleoptera	FA	−38	Burks & Hagstrum (1999)
Rhyzopertha dominica	Bostrichidae	Coleoptera	FA	−38	Burks & Hagstrum (1999)
Sigaus australis	Acrididae	Orthoptera	FT	45	Sinclair (2001)
Antarctopsocus jeanneli	Elipsocidae	Psocoptera	FA	47	Slabber & Chown (2004)
Paractora dreuxi	Helcomyzidae	Diptera	FT	47	Klok & Chown (2001)

Strategies: FT is freeze tolerant, FA freeze avoiding. Corrected latitude is rounded to the nearest degree. Negative corrected latitudes are in the northern hemisphere.

COMPARATIVE ANALYSIS

We updated Sinclair *et al*.'s (2003a) comparison of cold-tolerance strategies utilized by insects in the northern and southern hemispheres. The main data set was collected by Addo-Bediako *et al*. (2000), from an extensive search of the Anglophone literature on insect cold tolerance. Data were excluded from the database by Addo-Bediako *et al*. (2000) for methodological reasons (e.g. animals exposed to liquid nitrogen, or pierced by the thermocouple), or because the data came from summer-only collections or laboratory studies. The original data set of 241 northern hemisphere species (used in the Sinclair *et al*. 2003a study) was reduced by 2 after the discovery of a duplication not previously detected (a freeze-avoiding species), and the removal of a species for which the latitude of collection was not readily determinable (a freeze-tolerant species). From the literature, we added 19 new records from the northern hemisphere and 3 from the southern hemisphere (Table 2).

BOOTSTRAP

Distributions of cold-tolerance strategies were compared between the two hemispheres by assuming that the northern hemisphere represents a saturation of search effort, and is therefore an approximation of the global distribution of cold-tolerance strategies. Samples of 27 strategies (corresponding to the number of species studied in the southern hemisphere) were taken using a resampling-with-replacement protocol (Manly 1997) using a Visual Basic macro in Microsoft Excel. The distribution of proportions of freeze tolerance for 10 000 iterations were sorted, and two-sided confidence intervals defined from the distribution of resampled proportions. The macro is available from the corresponding author upon request.

Results and discussion

Of the 11 insect species that were examined, 6 were beetles and 5 cockroaches (Table 1). Eight of these 11 species were freeze tolerant, evidenced by a lower lethal temperature that is lower than the temperature of crystallization (Table 1), and also by direct observation of the release of the latent heat of crystallization (indicative of freezing of the body fluids) in individuals which were then observed to recover.

These results nearly double the data set of cold-hardiness strategies of southern hemisphere insects (from 13 to 24, cf. Addo-Bediako *et al*. 2000). In conjunction with three other recently published reports of cold tolerance in sub-Antarctic insects (see Table 2), these data demonstrate that 77% of the insect species examined for cold-hardiness in the southern hemisphere exhibit freeze tolerance ($n = 27$). The bootstrap analysis indicates that this proportion lies outside the 99·9% confidence interval for the distribution of strategies based upon the northern hemisphere data set. Thus, the prediction that insects in the temperate southern hemisphere are significantly more likely to exhibit freeze tolerance than their counterparts in the north is supported. An update of the northern hemisphere data

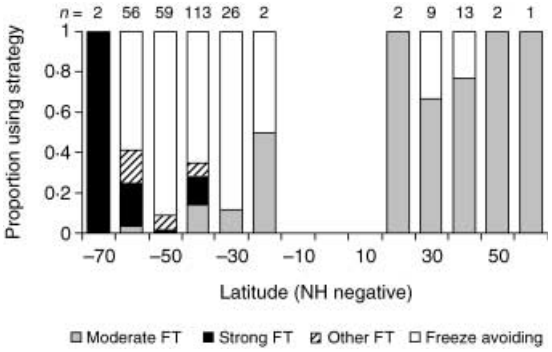

Fig. 1. Latitudinal distribution of insect cold-tolerance strategies published by 2003 (excluding species from 10° either side of the equator). Values above bars are sample sizes. Moderate FT = moderately freeze tolerant; Strong FT = strongly freeze tolerant; Other FT = other freeze tolerant (includes freeze tolerant with low supercooling point and species that survive only with external inoculation, also includes species for which data are inadequate to determine class of freeze tolerance). Data updated from Addo-Bediako *et al*. (2000) (shown in Tables 1 and 2); categorization is after Sinclair 1999).

set covering species published from 1999 to 2003 (19 new species, 2 of which are freeze tolerant, see Table 2) leaves the proportion of freeze-tolerant species unchanged at 29% (n = 258). Although there is a significant discrepancy in land–water ratio and number of studies between the hemispheres, the bias towards freeze tolerance in the southern hemisphere, and towards freeze avoidance in the north, is evident at all latitudes except the high arctic (Fig. 1), where the small number of species studied have all been shown to be freeze tolerant.

Sinclair *et al*. (2003a) suggested that selection for freeze tolerance in insects may differ between the northern and southern hemispheres. In the north, freeze tolerance evolves as a response to long, predictable and cold winters (Zachariassen 1985; Bale 2002), while in the south freeze tolerance is a flexible strategy, allowing insects to survive unpredictable cold snaps and to take advantage of warm periods without risks of mortality associated with the retention of ice-nucleating material in the gut. This means that, owing to mild winter temperatures and their fluctuation around 0 °C, southern hemisphere insects usually display 'moderate freeze tolerance' (Klok & Chown 1997; Sinclair 1999), i.e. they have a lower lethal temperature only a few degrees below the temperature of crystallization. By contrast, northern species are strongly freeze tolerant and survive temperatures well below their freezing point (Zachariassen 1985; Bale 2002). Moreover, freeze tolerance in northern hemisphere species is characterized by the same preparatory response to predictably low, subzero temperatures that is a feature of freeze-avoiding species (Bale 2002). Thus, different evolutionary pathways both to cold-hardiness and to freeze tolerance are characteristic of the insects inhabiting the mid-latitudes of the two hemispheres.

Biological invasions and deliberate introductions have led to an increasing homogenization of the world's pest species, many of which rely on specific overwintering stages (Bale 2002). For example, *Liriomyza huidobrensis*, added to the data set in Table 2, is an introduction to China, and it is unclear whether it comes from a northern or southern hemisphere clade in the Americas (Scheffer & Lewis 2001). The successful establishment of invasive species from between, as well as within, hemispheres is evidence that, regardless of the evolutionary pathways that may have led to the adoption of one or another strategy, these strategies can still provide for effective (although maybe not evolutionarily optimal) overwintering in other environments. However, according to our hypotheses, more cold-hardy species from the northern hemisphere should be limited by the variability of the mild south (and perhaps the increased energy expenditure of mild winters); whereas flexible southern species may be able to take advantage of milder winters in the changing climates of the north (IPCC 2001). It is premature to predict an influx of southern invasive species in the northern hemisphere, but the interaction between physiological flexibility, climatic variability and climate change is a key topic for long-term understanding of the way invasions are likely to unfold (see Mooney & Hobbs 2000; Stachowicz *et al*. 2002).

Mean annual air temperatures (maximum, minimum) for 2003–04 were 8·1 °C (23·2, –16·0) in the Drakensberg; 11·0 °C (31·1, –7·9) in the Cederberg and 13·4 °C (37·4, –7·3) in the Karoo. Mean winter temperatures were 1·9, 5·2 and 6·3 °C for the three sites, respectively, demonstrating the near-zero mean temperatures we predicted for variable southern hemisphere environments. Microclimate temperature recordings from the three habitats indicate that these relatively mild air temperatures are mirrored in the microclimates, resulting in repeated freeze–thaw events (Fig. 2). The minimum microhabitat temperatures recorded at each site between August and December 2003 were –11·5, –3·9 and –4·0 °C for the Drakensberg, Cederberg and Sutherland sites, respectively. In addition, Fig. 2b shows the effect of a cold front, when subzero temperatures and snow were experienced in the Cederberg on Christmas day (mid-summer) 2003.

The freeze-tolerant species presented in Table 1 would all be classified as 'moderately freeze tolerant' according to Sinclair (1999), and fall within the range of minimum temperatures recorded in the microhabitats, suggesting that selection is indeed responsible for the responses documented in these species. Although the minimum temperature observed in the Drakensberg is lower than the LLT of both species collected there, our animals were collected in December, and even in species that exhibit year-round freeze tolerance, there may be considerable seasonal acclimatization (Sinclair 1997). The flexibility, particularly with regard to winter feeding in southern species is also likely to mean that, although survival is an important aspect of overwintering, prewinter energy reserves will not play a great role in determining cold-tolerance strategy in this hemisphere, as has been proposed by

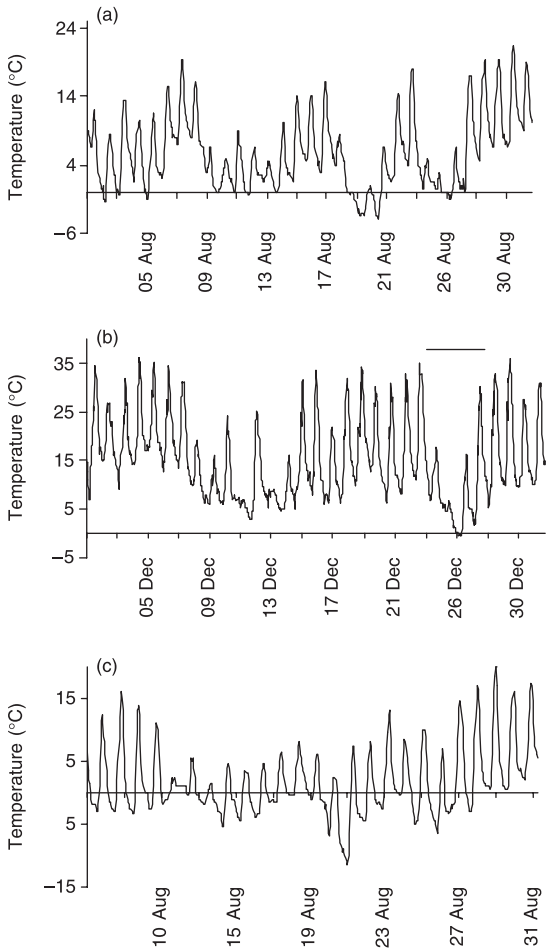

Fig. 2. Insect microhabitat temperatures from under rocks in (a) the high-altitude Karoo desert, (b) the Cederberg and (c) the Drakensberg for 1-month periods in 2003: (a) and (c) demonstrate considerable variability in microclimate temperature during winter, including considerable periods above 0 °C; (b) shows variability during mid-summer, with a cold frontal event indicated by the bar. Dataloggers and sites are detailed in Materials and methods.

Voituron *et al*. (2002) and demonstrated in the north by Irwin & Lee (2002).

The new data we present are heavily biased towards cockroaches and tenebrionid beetles, and therefore suffer in some respects from phylogenetic non-independence (see Harvey & Pagel 1991). Nonetheless, the beetle families Tenebrionidae and Carabidae include species that employ each strategy (Miller 1969, 1978; Strømme, Ngari & Zachariassen 1986; Salin, Vernon & Vannier 2003), and although all of the cockroaches from alpine and cold-temperate habitats in both hemispheres that have been studied are freeze tolerant (Duman 1979; Hamilton, Mullins & Orcutt 1985; Tanaka & Tanaka 1997; Block, Wharton & Sinclair 1998), some domestic species are known to have poor cold tolerance (Guthrie & Tindall 1968). Moreover, the diversity and abundance of cockroaches in the alpine zones of New Zealand (Johns 1966), South Africa (B. J. Sinclair, unpublished) and Australia (Green 1994) appear to be high compared with the northern hemisphere (Guthrie & Tindall 1968). A general predisposition towards flexible cold tolerance in cockroaches (at least in the south) may thus have facilitated their success in cold southern habitats, leading to phylogenetic non-independence of the fauna. In other words, this strategy might be a key innovation that has enabled cockroaches to radiate in southern alpine and temperate environments (see Chinn & Gemmell 2004 for an example). In such a case the link between the innovation and the exploitation of the environment would clearly be an adaptive one, though it would be considered phylogenetically non-independent, and therefore problematic, in a conservative interpretation (see Schluter 2000 for a general discussion of adaptive radiation). Thus, we consider the present results robust, but acknowledge that investigations of other groups would lend additional weight to them.

In conclusion, we have shown that insects in southern Africa, in keeping with other temperate species from the southern hemisphere, predominantly utilize freeze tolerance as their cold-tolerance strategy. This contrasts strongly with the temperate north, where freeze avoidance is the major cold-tolerance strategy employed by insects. It seems likely that the predominance of freeze tolerance in the southern hemisphere is a consequence of the climatic variability resulting from the large water–land ratio in the south. Hemisphere-related differences in the physiological and life-history characteristics of animals not only reflect widespread climatic differences between the hemispheres, but, as we and others (Gaston & Chown 1999; Russell 2000; Feild & Brodribb 2001; Chown *et al*. 2004) have shown, increasingly appear to be causally related to them. In the context of climate change and conservation, it is important that these differences are borne in mind when applying ecological lessons learned in one hemisphere to the other.

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